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Originals

Notes on the Spatial Genetic Structure among Populations of *Polytrichum commune* (Polytricaceae)

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Spatial distribution of genotypes was analyzed among 21 populations of a dioecious moss *Polytrichum commune* in the eastern United States using spatial autocorrelation analysis of enzyme polymorphisms. In a shorter distance (< 41km), three positive cases at $Mdh\text{-}3^{c,\,d}$ and $Pgm\text{-}1^{b}$ were significantly different from expected value, but none of significant negative value was detected. Beyond the distance class one (42 < 1,287 km), 11 significant negative values were detected in several alleles, indicating that gene flow, if low, might have operated among geographically close-spaced populations. However, the number of negative values (60%, 12 of 20 values) in the distance class one (0 < 41 km) indicates that genetic bottlenecks and/or founder effects may have played a role for shaping genetic structuring among populations. The results may reflect spores and vegetative fragments of mosses would be transported by air currents over moderately long distance.

Key words: allozymes, genetic structure, *Polytrichum commune,* spatial distribution

Biological features such as a probable short distance gamete dispersal (Wyatt 1985), autogamy in bisexual taxa, clonal reproduction, relativey short habit, and dominant gametophytic generation would lead us to expect low levels of gene flow among populations compared to small, herbaceous flowering plants.

There are routinely two indirect measures of gene flow among populations using allozyme as genetic markers. One estimate of the number of migrants per generation (Nm) is calculated based on F_{ST} (Wright 1951). Another estimate was based on the average frequency of private alleles (Slatkin 1985, Barton and Slatkin 1986). These models assume that alleles are neutral. Recently, spatial autocorrelation analysis has been applied to infer evolutionary processes among populations because it includes all pair comparisons in samples and it makes no assumptions about the spatial scale of structure among plant populations (Sokal and Oden 1978, Chung 1995, 1996).

Polytrichum commune Hedw., a dioecious moss, is widely distributed in temperate regions (Osada 1966). The species reproduces both sexually and asexually. In the eastern United States, *P. commune* grows widely on various substrates (soil, humus, and rock) in a variety of habitats such as meadows, edges of bogs, rock outcrops, mountain peaks, roadsides, and woodland trails. In this study we report the spatial structure among eastern north American populations of *P. commune* using allozymes as genetic markers.

Materials and Methods

A total of 713 individuals were collected from 21 populations of *Polytrichum commune* in the eastern United States (Fig. 1; Fig. 1 in Derda and Wyatt 1990). Small patches from discrete colonies were collected from each site until the site had been well covered. Sample size for each population was presented in Fig. 1. The data set (i.e., allele frequencies) used for analyzing spatial autocorrelation was obtained from a previous data set (Table 2 in Derda and Wyatt 1990). Enzyme extraction and electrophoretic procedures were described in Derda and Wyatt (1990) in which nine polymorphic (20 alleles) of 12 enzyme loci were resolved.

For spatial autocorrelation analysis, mean

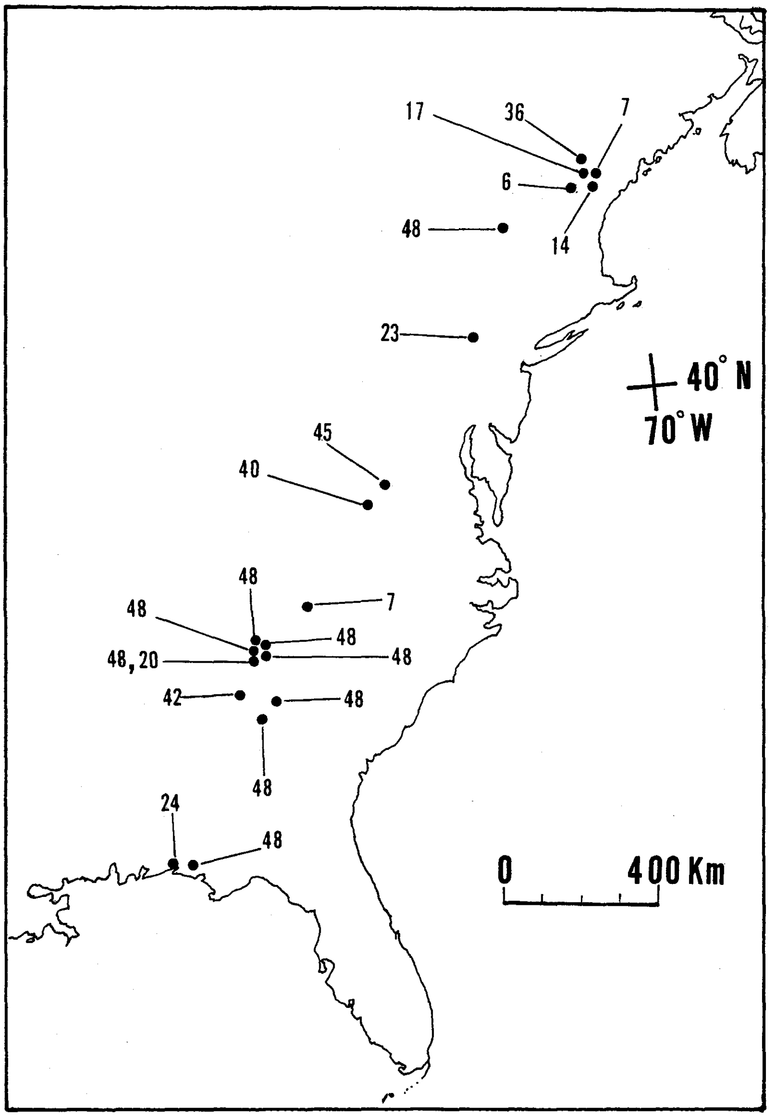

Fig. 1. The location of 21 sampled populations of Polytrichum commune in the eastern United States. Sample size is indicated for each population.

values were assigned to each population for the mean allele frequency values for alleles at each locus. Because only 21 populations of *P. commune* were analyzed and the diameter of each of the closely spaced population groups in the northern and southern regions (Fig. 1) was ca. > 70 km, eight distance classes, equalizing sample sizes among the distance classes. These distance classes were 0 < 41 km, 42 < 114 km, 115 < 305 km, 306 < 376 km, 378 < 644 km, 645 < 908 km, 909 < 958 km, and 959 < 1,287 km. Every possible pair of populations was considered as a join or a connection and was assigned to one of eight distance classes based on the geographic distance between them. Moran's *I*-statistic (Sokal and Oden 1978) was calculated for each of ten distance classes by interpopulational distance classes by

$$I_k = N\Sigma_{ij}\Sigma(W_{ij}Z_iZ_j)(W\Sigma Z_i^2)^{-1}$$

where: N is number of populations; the W_{ij} are elements of the join or weighting matrix, such that $W_{ij} = 1.0$ if the pair of ith and jth populations are in the distance class k and zero otherwise; $Z_i = X_i - X$, $Z_j = X_j - X$; the variables X_i and X_j are the genotypic scores for ith and jth populations, respectively; X is the mean score for all populations; and W is the sum of all W_{ij} for the distance class. Under null hypothesis, H_o, of a random distribution, I_K has expected value, μ_1, equal to $-1/(N-1)$ and expected variance, μ_2 (computational formula given by Sokal and Oden [1978] and Cliff and Ord [1981]). Thus, the statistic, $SND_K = (I_K - \mu_1)/\mu_2^{1/2}$, is a two-tailed test statistic of H_o, and it has an approximate standard normal distribution (Cliff and Ord 1981) under H_o. Thus, absolute values of SND_K greater than 1.96 and 2.58 are significant at levels 0.05 and 0.01, respectively. A significant positive value of I_k indicates that the pairs of populations separated by distances that fall within distance class k have similar genotypes (gene frequencies), whereas a significant negative value indicates that they have dissimilar genotypes (gene frequencies). Overall significance of individual correlograms was tested using Bonferroni's criteria (Sakai and Oden 1983). All calculations and statistical analyses were performed using the SAAP program (ver. 4.3) written by D. Wartenberg.

Results

A total of 20 alleles were used for spatial autocorrelation analysis. About 12% (160/919 cases) of Moran's *I* values for the eight interpopulational distance classes were significantly different from the expected value (E[*I*] = –0.05) (Table 1). In a shorter distance (0 < 41 km), three positive cases at *Mdh-3*$^{c, d}$ and *Pgm-1*^{b} were significantly different from the expected value (localities connected for that distance class had similar values of the three alleles), but none of significant negative values was detected (Table 1). Beyond the distance class one (42 < 1,287 km), 11 significant negative values were detected in several alleles, indicating that localities for that distance class had dissimilar values. However, only three (15%) of 20 alleles of the overall correlogram were significant (Table 1). These were *Mdh-3*$^{c, d}$ and *Pgd-1*^{e}. Average Moran's *I* values for the eight interpopulational distance classes were: 0.02, –0.05, –0.02, –0.08, –0.05, –0.09, and –0.05.

Discussion

A weak genetic structuring among populations existed for *P. commune* based on the intended 5% type I error; the proportion of significant Moran's *I* and overall correlograms were low (12% and 15%, respectively).

There was no typical monotonic decline from significant positive autocorrelation at a shorter distance to a significant negative autocorrelation at a longer distance. Monotonicity is expected when separation by dis-

Table 1. Spatial autocorrelation coefficients (Moran's *I*) of 20 alleles among 21 populations of *Polytrichum commune* in the eastern United States for the eight distance classes (1–8)

DB1) NP2) DC3)	41 26 1	114 26 2	305 26 3	376 27 4	644 26 5	908 26 6	958 26 7	1,287 27 8	*P*4)
Adh-1^{b}	–0.09	–0.07	0.01	–0.01	–0.03	0.00	–0.00	–0.21	0.593
Got-1^{b}	–0.15	–0.11	0.01	–0.07	0.01	–0.03	–0.11	0.05	0.682
Mdh-1^{b}	–0.01	–0.09	–0.03	0.05	–0.03	–0.16	–0.00	–0.11	0.963
Mdh-2^{a}	–0.07	0.28*	–0.11	–0.19	0.06	–0.08	–0.11	–0.16	0.089
Mdh-3^{a}	0.03	0.13	–0.09	–0.08	–0.04	–0.06	–0.15	–0.12	0.881
Mdh-3^{b}	–0.00	0.45	–0.08	–0.20	–0.04	0.01	–0.02	–0.11	0.408
Mdh-3^{c}	0.23*	–0.43**	0.37**	–0.26	–0.04	–0.16	–0.03	–0.08	0.041
Mdh-3^{d}	0.77**	–0.59**	–0.23	0.01	0.05	–0.10	0.10	–0.41**	0.000
Pgd-1^{a}	–0.07	0.01	0.19	0.06	–0.10	–0.32*	–0.01	–0.16	0.305
Pgd-1^{b}	0.04	–0.08	0.13	–0.13	–0.34*	–0.14	–0.08	0.19	0.295
Pgd-1^{c}	–0.12	–0.03	–0.36*	0.12	–0.08	–0.02	0.03	0.05	0.266
Pgd-1^{d}	0.01	–0.08	0.28*	–0.15	–0.10	–0.37*	–0.02	0.02	0.209
Pgd-1^{e}	–0.03	0.33**	–0.02	0.05	–0.03	–0.20	–0.17	–0.32*	0.023
Pgi-2^{a}	–0.17	–0.12	–0.03	–0.13	0.18*	–0.07	–0.15	0.08	0.172
Pgi-2^{b}	–0.15	–0.11	0.01	–0.07	0.01	–0.03	–0.11	0.05	0.682
Pgi-2^{c}	0.05	0.05	–0.11	–0.11	–0.23*	–0.07	–0.03	0.05	0.222
Pgm-1^{b}	0.22*	–0.22	–0.02	–0.02	–0.17	–0.07	–0.27	0.14	0.315
Pgm-2^{c}	–0.15	–0.11	0.01	–0.07	0.01	–0.03	–0.11	0.05	0.682
Pgm-2^{b}	–0.02	0.04	–0.12	–0.15	–0.29*	0.06	0.03	0.04	0.087
Pgm-2^{c}	0.02	–0.11	–0.30*	–0.33*	0.12	0.07	0.04	–0.12	0.194
Average	0.02	–0.05	–0.02	–0.08	–0.05	–0.09	–0.06	–0.05	

1)Upper distance bound.
2)Number of pairs.
3)Distance class.
4)Overall correlogram significance (Bonferroni approximation): *, $P < 0.05$; **, $P < 0.01$.

tance and gene flow among neighbor populations is the main factor. However, it is of worth to note that correlograms of *Mdh-3*^{d} and *Pgm-1*^{b} showed a "monotonic decline-like" pattern. In a shorter distance, three significant positive values were observed, but no significant negative value was observed. Beyond the distance class one (42 < 1,287 km), 11 significant negative values were detected at several alleles and in several distances. The results indicate that gene flow, if low, might have operated among geographically close-spaced populations. In the eastern United States, *P. commune* has a broader range and occurs in more diverse habitats (mountain tops, rock outcrops, bogs, or roadside ditches) than its congeners (Derda and Wyatt 1990). Although populations are somewhat isolated in the diverse habitats, the species is abundant and may have a "corridor" or belt to have more chance of gene movement into adjacent populations, particularly in mountainous regions. The number of negative values (60%, 12 of 20 values) in the distance class one (0 < 41 km), though not significant, indicates that genetic bottlenecks and/or founder effects, and asexual reproduction may have played a role for shaping genetic structuring among populations.

Gene movement could be occurred in mosses via sperm and spore dispersal and/or asexual propagules. Little is known about gamete dispersal distance and furthermore, nothing is known about effective spore dispersal distance of mosses (de Vries et al. 1983, Wyatt 1985, Hobbs and Pritchard 1987). The present results may support a suggestion by de Vries et al. (1983) that spores and vegetative fragments of mosses would be transported by air currents over moderately long distance. To clarify the fine–scale gene flow by spores, gametes, and/or vegetative fragments of mosses, more studies on the fine-scale spatial genetic structure should be conducted using allozymes and other molecular methods (e.g., a chloroplast DNA and amplified fragment length polymorphisms).

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G. S. デルダ[a], 鄭　明基[b]: ウマスギゴケ（スギゴケ科）自然集団の遺伝構造に関するノート

コケ植物のような配偶子による短距離散布を行う植物では，草本性の顕花植物よりも集団間の遺伝子流動は小さいと期待される．そこでアロザイムを遺伝的なマーカーとして，合衆国東部におけるウマスギゴケの21集団の遺伝的な構造を調べた．地理的な距離が短い場合（41 km以下）は3つの対立遺伝子座で期待値よりも有意に異なっていたが，マイナスの値は得られなかった．距離クラス1を超えると（42–1,287 km），いくつかの対立遺伝子座でマイナスの値が得られ，地理的に隔離された集団間では遺伝子流動の頻度が低いことを意味していると考えられた．しかし，距離クラス1（0–41 km）でマイナスの値が多いこと（60%）は遺伝的な分化が進んでいることを意味しており，集団の遺伝的構造にビン首効果と創始者の原理の双方あるいはそのどちらかが働いていることを示している．この結果は胞子や栄養体の気流にのってかなりの距離に渡って運ばれることによるものと思われる．

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